FINAL REPORT

Title: **Restoration synchrony of fuels and biodiversity in fire-excluded oak-hickory woodlands in north Mississippi**

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J. Morgan Varner
Pacific Wildland Fire Sciences Lab, USDA Forest Service Pacific Northwest Research Station, Seattle, WA

J. Stephen Brewer
Department of Biology, University of Mississippi, Oxford, MS

Jesse K. Kreye
Department of Forestry, Forest & Wildlife Research Center, Mississippi State University, Miss State, MS

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List of Abbreviations/ Acronyms

ANCOVA- Analysis of Covariance
ANOVA- Analysis of Variance
BWR- bark:wood ratio
DBH- Diameter at Breast Height (1.37 meters or 4.5 feet)
EMC- Equilibrium Moisture Content
NMDS- Non-metric Multidimensional Scaling
PCA- Principal Components Analysis
RAWS- Remote Automated Weather Station
SMC- Saturation Moisture Content
USDA- United States Department of Agriculture

Keywords

Duff, ecological restoration, flammability, fire effects, fire behavior, fuel moisture, functional restoration, *Liquidambar styraciflua*, mesophication, *Microstegium vimineum*, Mississippi, non-native species, oak-hickory woodlands, prescribed fire, *Quercus falcata*, *Quercus marilandica*.

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Abstract

Widespread fire exclusion and land-use changes have dramatically impacted the former oak (*Quercus* spp.) savannas, woodlands, and forests of eastern North America. Primeval woodlands were characterized by open canopies of a diversity of oaks (*Q. alba, Q. falcata, Q. coccinea, Q. stellata,* and others) and hickories (*Carya tomentosa, C. pallida,* and others) and species-rich herbaceous understory communities. Fire exclusion largely eliminated shade-intolerant herbs and shifted the composition of the overstory toward more fire-sensitive mesophytic trees that are hypothesized to diminish fire behavior, a positive feedback process termed "mesophication". We took advantage of a long-term restoration project in north Mississippi to ask a series of questions related to the efficacy of restoration: *i*. which functional groups of fuels drive surface fire behavior; *ii*. how does flammability change across a mesophication gradient; *iii*. are there plant species traits that predict success or persistence in fire-prone sites; *iv*. how do restoration treatments impact non-native herbs; and *v*. how do restoration treatments impact overstory oak growth? The studies took place in oak-hickory and oak-hickory-pine ecosystems in north Mississippi.

Using understory vegetation and fuels data, we mapped fire behavior in the thin+burn site. Fire behavior (a composite using Principal Components Analysis) was best predicted by herbaceous cover, and specifically two asters and a grass species. Other functional groups that included native vines and specific forbs diminished fire behavior. As restoration treatments favor these pyrophytic forbs and grasses, fire behavior will overcome the past effects of fire exclusion.

Leaf litter fuels from fire-tolerant and fire-intolerant trees was also compared via laboratory drying and burning experiments. Litter from pyrophytes (oaks and hickories) burned with greater intensity than mesophytes (sweetgum, cherry, and elm) and these differences were magnified when differential drying rates were included. We combined flammability traits with physiological and protective (bark accumulation and wound recovery) data in a meta-analysis to evaluate potential trade-offs between traits. In 9 oaks with sufficient data, we detected strong patterns in protection, flammability, and growth where pyrophytes experienced less growth, but invested in defensive bark traits and offensive flammability traits that enabled their survival in frequent fires. Mesophytes invested in growth at the cost of defense and flammability. When we further evaluated bark traits, we found that in addition to differential allocation by species, that traits such as bark surface area, volume, and the relative vertical allocation of bark differed. We evaluated the effects of restoration treatments on overstory oaks and found that different oak species responded differently to thinning and burning. Southern red oak experienced greater radial growth following restoration than post oak, which suffered reduced growth. Lastly, we measured how restoration treatments affected the embedded non-native grass *Microstegium vimineum*. The non-native grass increased following burning, an unintended consequence of restoration activities and a complication for managers.

Our results collectively point to the effectiveness of thinning and burning for restoring fire behavior and the synchronous recovery of understory plant diversity. The observed increases in the non-native grass complicate this story, but their extent at present is restricted and should not diminish the application of prescribed fire in oak woodland restoration.

Objectives

This research was tied to two of the Task Statement questions:

1) **Metrics**- *What metrics have been used to characterize the effectiveness of fuels treatments at meeting ecosystem restoration objectives*? *What are the characteristics of useful metrics*? *Which metrics have potential for effective and broad usage*?

2) **Scale**- *How do vegetation management and fuels treatment effects on ecosystem restoration vary by spatial and temporal scale*? *At what scales can vegetation management and fuels treatments be effective at meeting ecosystem restoration objectives*?

We specifically focused on 1) melding traditional metrics used in plant community restoration with fuels metrics and 2) evaluating how coincidental in space and time the recovery of plant diversity (a main restoration goal) and fuelbed recovery (a fuels treatment goal) were. We coupled these metrics with more in-depth analyses of the marginal effects of species compositional changes on community flammability and on traditional metrics of restoration "success", such as overstory tree growth and changes in understory non-native species.

There were changes in the PIs affiliation that delayed the project and issues with state bans on prescribed burning that limited our ability to answer each, but we feel our supplemental work made up for the delays and limited field fire measurements.

The specific hypotheses we tested included:

H1: Plant community metrics (e.g., alpha species richness and cover of species with fidelity to open woodlands) are correlated with fire behavior metrics (flame length and fuel consumption).

H2: Restoration treatments (thinning and burning) will change surface litter composition from a mixture of remnant pyrophytes and invading mesophytes to more pyrophytes. Additionally, burning and thinning will result in reductions in duff and fuel depths.

H3: Pyrophytic litter will dry faster and burn with greater intensity than litter from mesophytes.

H4: Bark will accumulate faster and be more concentrated within the flaming zone on pyrophytic trees than on mesophytes.

H5: Fire-adapted protective and offensive traits will come at a cost to growth and other physiological measures.

H6: Residual overstory oak trees will increase in growth following restoration treatments. Further, these differences will be magnified during dry year and moderates during years when burning takes place.

H7: Native understory herbs will increase following restoration treatments.

H8: The non-native grass *Microstegium vimineum* will expand following restoration treatments, particularly in burned areas.

Collectively, these research questions seek to fill a void in the understanding of the linkages between restoration treatments and vegetation-fire behavior-fire effects relationships. These results will be of relevance beyond Mississippi to other oak-hickory sites and perhaps more broadly where restoration and fuels treatments seek to reverse the effects of fire exclusion.

Background

Fire-maintained woodlands were an important and extensive component of the landscape throughout the eastern United States prior to European settlement (Nowacki and Abrams 2008, Stambaugh et al. 2015, Varner et al. 2016a). The vast majority of these ecosystems have experienced significant declines and degradation across most of their extent. In pyrogenic oak-hickory (*Quercus-Carya*) dominated woodlands in the southeastern U.S., a major driver of degradation is fire exclusion, which facilitates the invasion and establishment of fire-sensitive species (Nowacki and Abrams 2008). These fire-sensitive species can in turn reduce the flammability of the community through a positive feedback process termed "mesophication" due to the lower flammability litter, faster decay rates of litter and woody debris, and alteration of microclimates to promote dampened forest floor fuel conditions (Nowacki and Abrams 2008, Kreye et al. 2013, Mola et al. 2014). The consequences of mesophication are altered hydrology and cation availability (Alexander and Arthur 2008), degraded plant diversity (Brewer et al. 2015), and losses in game and non-game animal habitat (Harper et al. 2016).

Restoration treatments in the region generally target the removal of selected fire-sensitive (i.e. mesophytes) tree species, however the effectiveness of these treatments on fuels and flammability have not been well-studied (McEwan et al. 2010). As efforts to restore fire-maintained woodlands proceed, it is critical to develop an understanding of how restoration changes community flammability (Stambaugh et al. 2015). The legacies of mesophication include altered species composition (invasion and success of mesophytic trees) that cascades to altered fire behavior and muted effects. Because of these and other issues, restoring and using fire in eastern deciduous forested ecosystems is far from settled (McEwan et al. 2010, Matlack 2014, Stambaugh et al. 2015, Matlack 2015, Varner et al. 2016). Questions remain in eastern oak-hickory restoration revolving around the effects of fire on species diversity, how species persist in frequent fire regimes, how mesophytic invaders affect ecosystem processes, and the potential unintended consequences of prescribed fire and restoration treatments.

Our objectives were to examine the effects of restoration (selective cutting and prescribed fire) on site flammability by examining surface herbaceous and litter species fuels composition in a southeastern oak-hickory woodland. Beyond characterization, we also investigated the effects of canopy shade and microclimate on fuel moisture dynamics. We combined moisture dynamics and lab flammability methods to evaluate the effects of mesophytic invasion. We coupled this fuel work with questions related to the invasion by a non-native grass, *Microstegium vimineum*. We additionally sought to understand the growth responses of overstory oaks to restoration treatments. These studies provide information to assist with major needs of regional managers and should strengthen the foundation for restoration and management of fire-prone oak-hickory ecosystems.

Materials and Methods

Study Area and Ecosystem

Study Areas

Strawberry Plains Audubon Center
An oak-hickory woodland restoration experiment was initiated in 2003 at Strawberry Plains Audubon Center (hereafter, “Strawberry Plains”), a 1,000-ha sanctuary located in the loess plains of north-central Mississippi. The loess plains are characterized by gently rolling hills with moderately fertile, mesic silt and sandy loams in the uplands and floodplains. The experiment was a paired design (adjacent 1 ha treated and control areas) replicated at each of two upland mesic sites 2 km apart (the Wildflower site [34°49'60" N, 89°28'32" W] and the Sharecropper site [34°49'52" N, 89°27'17" W]). Both sites contained a mixture of silt loam alfisols and sandy loam ultisols, with silt loam predominating at Wildflower, and sandy loam predominating at Sharecropper (Morris 1981, Maynard and Brewer 2013). At the beginning of the experiment, both sites contained closed-canopy (> 90% overstory canopy coverage), mature oak-hickory-sweetgum-elm forests (100-150 + years old trees at Wildflower, 50 + years with scattered 100 + year-old trees at Sharecropper), long protected from fire. Dominant overstory and midstory tree species included southern red oak (*Quercus falcata*), post oak (*Q. stellata*), black oak (*Q. velutina*), white oak (*Q. alba*), blackjack oak (*Q. marilandica*), mockernut hickory (*Carya tomentosa*), sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), and winged elm (*Ulmus alata*) (Brewer 2014). Aerial photos from the early 1960s revealed that the forest at Sharecropper was more open than at Wildflower, with the former showing some signs of soil erosion caused by prior cotton agriculture upslope dating back to the 1800s.

Tallahatchie Experimental Forest
The second study site was located in an upland oak-pine forest within the Tallahatchie Experimental Forest (hereafter “Tallahatchie”), the site of long-term monitoring of oak-pine forest dynamics (Surrette et al. 2008, Brewer et al. 2012, Cannon and Brewer 2013, Brewer 2015). The Tallahatchie is located within the northern hilly coastal plain of Mississippi (within the Greater Yazoo River Watershed; 34° 30′ N, 89° 25′ 48″ W). Soils in the upland forests are acidic sandy loams and silt loams on the ridges, and acidic loamy sands on side slopes and in the hollows (Surrette and Brewer 2008). In the early 1800s, before extensive logging and modern fire exclusion, open stands of fire-resistant tree species such as blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), Southern red oak (*Q. falcata*), black oak (*Q. velutina*), and shortleaf pine (*Pinus echinata*) dominated the upland landscape (Surrette et al. 2008). Following fire exclusion in the twentieth century, the overstory of second-growth forests became dominated by a mixture historically dominant upland oak species, except blackjack oak, shortleaf pine, some species historically common in floodplains (e.g., white oak [*Q. alba*], sweetgum [*Liquidambar styraciflua*]), and some species that were common in both uplands and floodplains historically (e.g., hickories [*Carya* spp.]; Surrette et al. 2008]. After decades of fire exclusion in the mid to late 1900s, but prior to damage by a tornado in 2008, the sapling layer in all stands at Tallahatchie was dominated by blackgum (*Nyssa sylvatica*), hickories, black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and sweetgum. After damage by the 2008 tornado, damaged stands with open canopies at Tallahatchie contained these non-oak species and saplings of various oak species, including the aforementioned plus scarlet oak (*Q. coccinea*; Cannon and Brewer 2013).

Field and Lab Methods

The role of restored groundcover vegetation on forest floor fire behavior

Using the established plot network, we quantified fuels, vegetation, and fire behavior during a winter prescribed burn in the thinned/burned treatment at the Wildflower site at Strawberry Plains. Twenty-one vegetation plots (1.5 m × 1.5 m) were surveyed for plant species composition and density prior to burning. We supplemented these vegetation data with depths of leaf litter and duff and cover of fuel functional groups (forbs, grasses, woody fuels, leaf litter, and bare ground) prior to burning. Vegetation data were analyzed using cluster analysis and indicator species analysis on species density.

Fire behavior was quantified in a diversity of ways. Flame lengths were ocularly estimated in each plot during burning using aluminum height poles marked with 10 cm graduations at two locations per plot and averaged. We estimated fuel consumption via direct measurement of duff and litter consumption (depth reduced and %) and by consumption of pre-weighed oven-dry and field moisture 1- and 10-hr dowels. We supplemented these measures with changes in forest floor cover (%) and the coverage of white ash (%) post-burn. We combined all of these measures of fire behavior into a principal components analysis (PCA). The resulting fire PCA and vegetation data were combined in a non-metric multidimensional analysis to reveal species patterns and general community fire behavior.

Temperature and relative humidity during prescribed burning ranged from 0.8° C to 3° C and 37% to 43%, respectively. Winds were light (1-5 km h^{-1}) and variable. Three days prior to burning, 12 mm of rain was recorded at the Windborn, Mississippi RAWS (28 km away). Moisture content of litter measured immediately prior to ignitions averaged 32%. Burning was conducted using strip-head firing with intervals between successive strips between 10 and 20 m apart.

Effects of fire and thinning on surface litter, woody, and duff fuels

We evaluated the effects of restoration on surface fuels at Strawberry Plains in the control and thin+burn plots at Wildflower and Sharecropper. Litter was collected in ten 1 m × 1 m frames randomly distributed throughout each plot. Four samples per plot were then randomly selected in the lab and sorted to separate out non-leaf material and all leaves that were identifiable to the species level and oven-dried. Downed woody fuels were measured in seven planar intercepts (extending in random directions from systematically distributed start points) per site. Litter, duff, and fuelbed depths were measured along each plane.

Fuels were compared using a variety of complimentary methods. We calculated percent similarity between plot litter species composition using the Bray-Curtis coefficient on plot averages of dry litter weight percent per species. Site differences in fuels (1-hr, 10-hr, 100-hr, 1,000-hr, and duff) were analyzed using ANOVA or the non-parametric Kruskal-Wallis test when assumptions of normality and equal variance were not met. When differences were detected, a post-hoc Tukey-Kramer or Kruskal-Wallis z-tests (non-parametric) were used to isolate pair-wise differences.

Effects of fire and thinning on litter moisture dynamics

To estimate the diel (24-hour) fuel moisture dynamics across restoration treatments, we sampled forest floor fuel moisture on 25 July 2016 (growing season) and 13 December 2016 (dormant season) across the thin+burn treatment, burned only treatment, and control at the Wildflower site at Strawberry Plains. Twenty-five mm of rain was recorded at the nearest RAWS (28 km away) in the 7 days prior to summer sampling (16 mm the day before) and 29 mm of rain over the 7 days prior to winter sampling (12 mm the day before). No rain was recorded on either sampling days. Temperature and relative humidity ranged from 23 to 35 °C and 44 to 96% during the summer sampling period. The winter sampling period was cooler (2 to 12 °C) and moister (84 to 98% relative humidity). Solar radiation reached 980 W m^{-2} on the day of summer sampling, but only reached 200 W m^{-2} on the day of winter sampling. We collected surface litter every 3 hours between 0900 and 0600 at the base (basal) and beyond the dripline (open) of eight dominant oaks (four post oak, four southern red oak) in each of the three sites. We conducted a preliminary analysis of litter moisture across treatment and sampling location (basal *vs.* open) for each sampling season separately.

Effects of mesophication on litter flammability

We compared the litter flammability of pyrophytes, mesophytes, and across the sequence of mesophication. At the Wildflower site at Strawberry Plains in December 2016, we collected eight litter samples from locations surrounding the bases of 24 randomly selected dominant oaks as well as eight samples beyond their dripline to ensure capture of other species' (*Carya* spp. and mesophytes) litter. We used the collected litter to create sixty fuelbeds (15 grams each) comprised of four relative contributions of mesophytic and pyrophytic litter (0, 33, 66, and 100% mesophytes by weight) representing a gradient of increasing dominance by mesophytic litter.

Litterbeds were burned in a 4 × 3 experimental design (4 litter-composition treatments and 3 moisture treatments: wet, moderate, and dry). All litter was oven dried at 60 °C and allowed to equilibrate to laboratory conditions (24 to 28 °C, 40 to 50 % relative humidity) prior to experiments. Moisture treatments consisted of defined drying times, allowing moisture desorption to vary across litter compositions. For wet and moderate moisture treatments, we soaked litter in water for 24 hours to reach saturation moisture content (SMC) and allowed samples to dry for 12 h for the wet treatment and 24 h for the moderate treatment. The dry treatment consisted of all litterbed mixtures at equilibrium moisture content (EMC), allowing us to compare the exclusive effect of composition on flammability.

We burned litterbeds at Humboldt State University Wildland Fire Science Laboratory (Arcata, California, USA) using established methods. Maximum flame height (cm), flaming time (sec), smoldering time (sec), and consumption (%) were measured for each burn. We combined correlated metrics using principal components analysis (PCA) and compared PCA scores across moisture and litter composition treatments using general linear modeling. We also conducted an ANCOVA to evaluate whether flammability metrics differed across litter composition after accounting for moisture content. Post-hoc multiple comparisons of means were conducted using the Tukey-Kramer Test for all analyses.

Response of overstory oaks to fire and thinning restoration treatments

We evaluated the effects of restoration thinning and burning at the Wildflower site at Strawberry Plains. During the summer of 2016, 11 southern red oak and 11 post oak trees were selected within each of the thin+burn and control stands. Two tree cores were extracted from each selected tree at DBH taken 90° apart from each other. Collected tree cores were air dried, mounted, and sanded until cellular structures became visible in the cross-sectional view under magnification. Two cross-dated tree-ring chronologies were developed for each species. Each chronology was developed using all 22 trees (44 cores) from across both stands. Annual tree ring-widths were measured under stereoscopic magnification to the nearest 0.01 mm using the Velmex Measuring System and J2X software (v.3.2.1, 2004). Dated tree-ring width measurement values were verified to ensure quality of visual cross-dating using COFECHA software and any dating errors were corrected.

To determine if changes in radial stem growth occurred following implementation of recurrent thinning and burning treatments, we compared mean annual ring width and total radial growth increment for the 11 years prior to and following treatments. Comparisons were made between pre- and post-treatment values (mean ring width and total 11-year radial growth) for each individual species using Wilcoxon-Mann-Whitney tests. To determine if radial growth responses differed between species, we calculated the relative percent growth change in total 11-year radial growth increment from pre- to post-treatment implementation for southern red oak and post oak. Relative percent change in growth was compared between southern red oak and post oak in both the control and thin+burn stands using a Wilcoxon-Mann-Whitney test.

Suites of fire-adapted traits

Bark study

We studied bark allocation at the Tallahatchie Experimental Forest. We selected 10 juvenile trees of seven species for destructive stem analyses. The species included shortleaf pine (*Pinus echinata*), loblolly pine (*P. taeda*), blackjack oak (*Quercus marilandica*), southern red oak (*Q. falcata*), mockernut hickory (*Carya tomentosa*), black cherry (*Prunus serotina*), and blackgum (*Nyssa sylvatica*), all common and dominant species in the area. Cross-sections were cut along the stem every 10 cm from the base (0 cm) to 100 cm and every 20 cm from 100 cm to 200 cm. Each cross-section was sanded with up to 1000-grit sandpaper and aged. Cross-sections at 0 and 140 cm heights along with sections from each age break were digitally scanned on a flatbed scanner. Total area, outer and inner bark area, and wood area were measured using ImageJ image analysis software.

Regression analyses for each species were conducted on ground-level cross-sections. We compared both outer and inner bark area versus wood area to see how these measurements change with increasing stem size. We conducted a PCA using age, height, height growth (total height/age), inner and outer bark area, wood area, bark:wood ratio (BWR), and bark roughness (1 – total area/convex hull area) as variables. Lastly, we conducted a mixed-effects model on all cross-sections to test the model: BWR = MHT*Species, where MHT is the measured height along the stem. A unique tree number for each individual was included as a random effect because multiple measurements on the same individual are not independent.

Meta-analysis of Traits

To evaluate species-level traits of a broader set of southeastern oaks, we used published data on traits for eight oak species that span gradients in stature (from small to large trees), leaf lifespan, longevity, apparent site preferences (mesic to xeric), and represent the phylogenetic diversity of the genus. Flammability data were taken from Kane et al. (2008) and Varner et al. (2015b). Oak litter drying data (drying time and moisture holding capacity) were taken from Kreye et al. (2013) and Mola et al. (2014). Oak bark thickness and wounding response data were derived from Jackson et al. (1999) and Romero et al. (2009). We used oak physiological data from Cavender-Bares et al. (2004a).

We combined traits (flammability, protective, and physiological) using PCA. We subsequently compared the relationships among trait groupings via correlations between factor scores from each of the retained protective, flammability, and physiological trait axes. In resulting comparisons, we discuss all axis relationships with $r \geq 0.60$. To evaluate the suites of traits among the group of eight oaks, we used a PCA to reduce dimensionality of the 25 traits available for all eight species and subsequently conducted a cluster analysis, by species, using the resulting flammability, protective, and physiological PCA axes. To determine the optimum number of clusters, we used fuzzy agglomerative clustering.

Effects of restoration treatments on native groundcover and Microstegium vimineum

To evaluate the effects of restoration treatments on groundcover and an invasive grass, we established plots at the Wildflower and Sharecropper sites at Strawberry Plains. In fall and spring censuses, we made approximate counts of all groundcover plant species within 10 × 30 m subplots nested within adjacent treated and control plots (~0.6 to 7.4 ha) at each of the two sites. To ensure a representative sample of the number of species within each plot, statistical analyses of species richness were based on estimated expected numbers of species derived from species-area curves within each plot and used the experimental error (plot-level) term with 1 df (2 sites and 2 treatment levels). Groundcover species composition was quantified by density (counts of stems or clumps of all species) and fidelity of the sub-subplot assemblage to open habitats, forests, and disturbed habitats. Habitat fidelity calculations were derived from weighted averages of abundances of all species, wherein the weights were species-specific habitat indication scores. Statistical analyses of density and habitat indication were done using nested ANOVA using a Restricted Expected Maximum Likelihood approach

Japanese stiltgrass, *Microstegium vimineum*, though common in forests at Strawberry Plains and present within the sites currently, was absent from groundcover plots in this study. Therefore, beginning in 2007, thorough searches for patches of Japanese stiltgrass (clumps of more 20 plants within a ~4-m^2 area) were conducted throughout each treated and control plot at each site to monitor changes in density within patches and the proliferation or disappearance of patches in response to restoration treatments. Counts of Japanese stiltgrass were made at the time of patch establishment and then repeated yearly in the fall and spring until 2014. In very dense patches (i.e., > 500 stems), total density was estimated by systematically locating eight points within the patch and measuring the distance between each point and the closest Japanese stiltgrass stem. Changes in abundance of Japanese stiltgrass were analyzed statistically by first taking the difference of natural-log transformed densities per m^2 for the initial and final census for each patch and then analyzing the effects of treatment, site, and the treatment by site interaction using patch variation nested within site and treatment as the error term. Treatment and site effects on the rate of patch proliferation of Japanese stiltgrass were examined statistically using randomization tests. Differences between the treated and the control plot were tested at each site, as were differences in the difference between treated and control plot between sites. Responses of groundcover vegetation within patches of Japanese stiltgrass over time were analyzed by examining the responses of species richness and log-transformed densities to site, treatment, site × treatment and the product of Japanese stiltgrass density and patch age using ANCOVA. Responses of the native vegetation were examined by quantifying both the change between initial and final censuses and the average of the initial and final censuses.

Groundcover restoration with fire and a tornado disturbance

To evaluate the effects of fire and more severe overstory disturbance on groundcover communities, we measured vegetation responses at Tallahatchie following an EF-4 tornado and repeated prescribed fires. The study contained four ~1 ha study plots in which tree, sapling, and groundcover vegetation composition had been monitored since 2006 and before (back to 1998 for two plots). A discriminant function analysis involving 11 variables, including: percent canopy cover; leaf litter percent cover; percent soil disturbance from tip-ups; percent bare ground; percent cover by dead and downed crowns; percent cover by live, downed crowns; sand to silt ratio; percent clay; percent organic matter; and elevation revealed that percent canopy cover was the most important distinguishing environmental variable between damaged and undamaged portions of the plots in 2009.

The herbaceous groundcover vegetation plots established in 2006 or earlier were revisited and censused. The censuses consisted of fall and spring censuses. Initial censuses involved approximate counts of all groundcover plant species within two 10 m × 30 m subplots located on the upper slope or the lower slope, nested within each plot. Beginning in 2009, more precise counts of groundcover plant abundance were conducted within each 10 m × 30 m subplot by subdividing the subplots into eight 5 m × 7.5 m sub-subplots. Counts were converted to seven abundance classes: 1 (1 to 15), 2 (16 to 31), 3 (32 to 79), 4 (80 to 159), 5 (160 to 319), 6 (320 to 543), and 7 (>543). Habitat fidelity calculations were derived from weighted sums of abundances of all species with habitat indicator values of greater than 0 for a given habitat category, wherein the weights were species- specific habitat indication scores.

To examine pre-storm differences on groundcover vegetation, one-way ANOVA were used on plot-level differences in plant species richness before the tornado. To examine initial differences in groundcover vegetation between subplots that were severely damaged versus those that were not, subplot differences in species richness and weighted summed abundances of positive habitat indicator species were compared after the tornado but before the 2010 prescribed fires using ANOVA. To examine the effects of tornado damage and fire on changes in vegetation over time, differences among the four different damage and fire combinations were analyzed using repeated measures ANOVA.

Results and Discussion

The role of restored groundcover vegetation on forest floor fire behavior

The restored site at Wildflower burned with highly variable intensity and spread rates and was driven by small-scale differences in surface plant composition (Fig. 1). Using our combined PCA for fire intensity overlaid on a NMDS plot of fuel species, we found that hot spots were most closely related to perennial forbs (particularly asters), native *Dichanthelium* grasses, and native warm season grasses (*Andropogon virginicus*, *Schizachyrium scoparium*, and *Saccharum giganteum*). Species than diminished fire intensity and spread included native ferns, shrubs, vines and trailing herbs, and other perennial forbs.

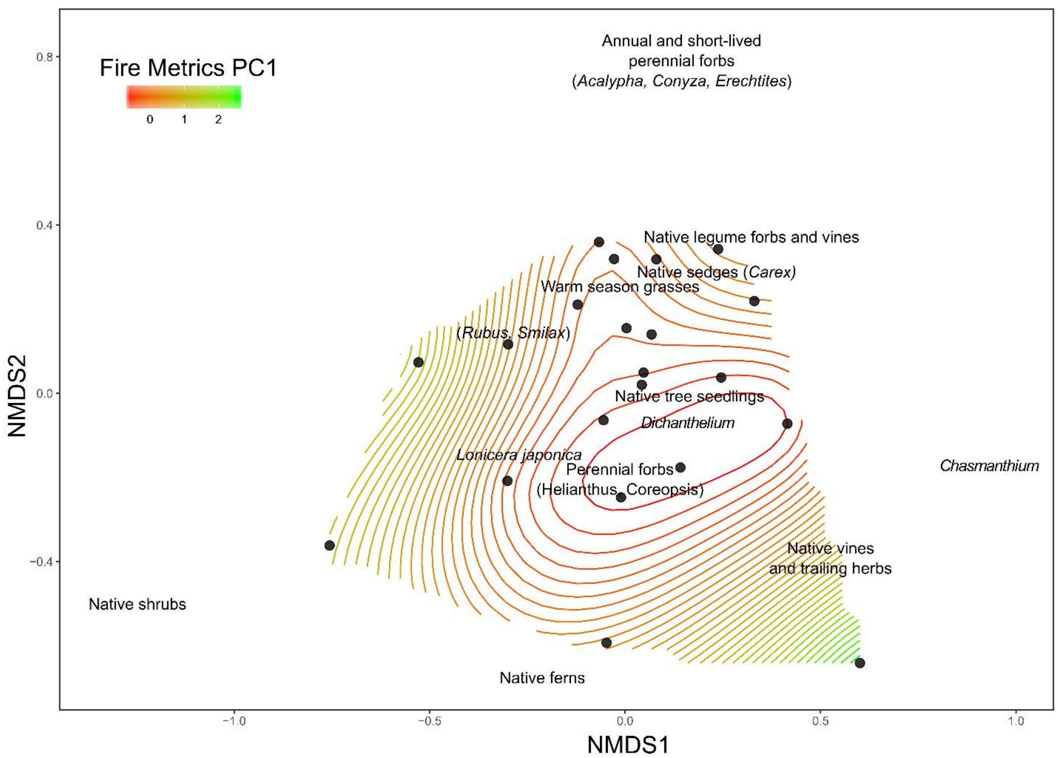

Figure 1. Nonmetric Multi-Dimensional Scaling (NMDS) ordination of vegetation density in 21 subplots at the Strawberry Plains Audubon Center. A 2-dimensional solution was chosen with a final stress of 0.18. The contour surface is the result of fitting a smooth surface for the first principal component of the fire metrics data onto the NMDS ordination (R^2 = 0.83, P < 0.0001). Warm season grasses include *Andropogon virginicus*, *Schizachyrium scoparium*, and *Saccharum giganteum*.

Restoration treatments led to establishment of several of the pyrophilic herbs, particularly the asters, and native *Dichanthelium* and warm season grasses, a common restoration outcome across the region (e.g., Brewer et al. 2015). The degree to which these species cover restored woodlands, in combination with litter contributed by remnant overstory pyrophytic oaks and hickories will functionally restore the intensity and spread of fire to maintain these restored ecosystems. The simultaneous release of residual vines (particularly *Vitis rotundifolia*), shrubs, and small resprouted trees will concurrently dampen fire behavior and resulting effects. This polar response complicates restoration activities (McEwan et al. 2011). Future attempts to diminish these fire dampening species, whether via repeated prescribed fires or chemical (targetted herbicides) or mechanical methods will determine the long-term success of regional restoration activities.

Effects of fire and thinning on surface litter, woody, and duff fuels

There were clear changes in litter species composition and diversity after the restoration treatments. The richness of identified litter species decreased in treatments at both sites. The controls at each site had 14 and 16 overstory species, while the plots thinned and burned had only 8 and 12 species. Thinning and burning resulted in greater dominance of the fuelbed by flammable red oak litter. Southern red oak, blackjack oak, and scarlet oak are known to be highly flammable (Varner et al. 2015), with characteristically rapid drying (Kreye et al. 2013) followed by high intensity flaming combustion of their curled litter. The Wildflower control and treatment were 39% similar in the relative contribution of different species to leaf litter. The Sharecropper control and treatment were slightly more similar (45% similarity). The two controls were 58% similar, whereas the two restoration treatments were 33% similar. At Sharecropper the contribution of hickory remained similar, at 6.9 and 7.6% for the control and treatment respectively. At Wildflower, however, the contribution of hickory decreased from 6.7 to 2.2% in the control and treatment. Classical mesophytic species such as red maple did not comprise a substantial portion of the litter bed even in control plots, generally contributing less than 10% of the litter bed combined.

Woody fuels did not generally differ between sites, however there were significant differences detected for duff depth ($p=0.014$) and 100-hr fuels ($p<0.0001$). Wildflower, but not Sharecropper, had significantly lower duff depth in the thin+burn treatment than in the control. Wildflower, but not Sharecropper, also had lower 100-hr fuel loading in the control than in the thin+burn. While it might be expected that the restoration treatments would have lower woody fuels loading due to consumption in prescribed fires, the restoration methods likely resulted in an ongoing influx of woody material due to girdling and overstory mortality caused by fires. This slow attrition likely resulted in the significant increase in 100-hr fuels in the treatment plot at Wildflower. Sharecropper appeared to have a similar pattern, however the variation was too high for the differences to be significant. As killed trees fall and recruit to the surface, patchy increases in fire severity will likely occur.

The protracted fire-free period prior to restoration resulted in accumulation of forest floor litter and duff. Wildflower had a significantly thinner duff in the restoration treatment while no differences were detected at Sharecropper.

The components examined in this study are only a small part of the broader picture of community flammability. Fuel moisture changes caused by canopy opening, changes in herbaceous understory biomass and cover, and potential effects of varying leaf litter mixtures are other key factors that need to be examined in order to get a better picture of changing fire potential with restoration of this woodland. As restoration treatments continue, it is important to consider and evaluate whether these treatments are actually restoring functional site flammability to desired levels. Through increases in dominance of litter by high flammability red oaks and increases in 100-hr fuels restoration treatments are increasing the flammability of these oak-hickory woodlands. As litter contributions shift over time, these species may facilitate surface fires at frequencies recorded across the region and maintain species dependent on open woodlands (Stambaugh et al. 2015).

Effects of fire and thinning on litter moisture dynamics

We found distinct patterns in our diel sampling of litter moisture dynamics at Strawberry Plains. Litter moisture decreased throughout the day and recovered partially overnight across all sites in both seasons. Differences between treatments (thin+burn, burn only, and control) were only detected during daytime sampling in winter (Fig. 2). Litter in thin+burn treatments were drier than both burn only and control plots on 13 Dec 2016, but litter moisture became similar at night. Litter location (basal vs. open) did not influenced moisture contents on either sampling days.

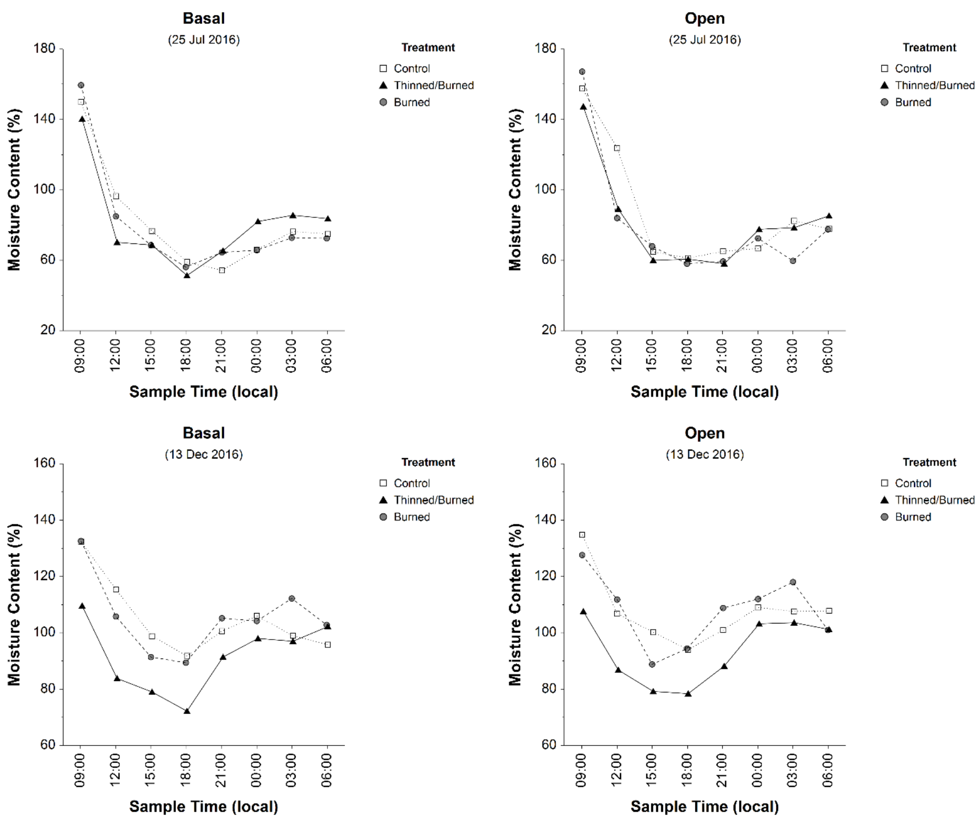

Figure 2. Forest floor litter moisture in treated (thinned/burned, burned only) and untreated (control) oak-hickory woodlands where fire was excluded for several decades prior to treatments. Sampling occurred over a 24 h period in summer (above) and winter (below) and litter was collected at the base of dominant oak trees (left) and in the open beyond their driplines (right).

Changes in overstory composition and structure resulting from encroachment by fire-sensitive mesophytes into pyrophytic *Quercus-Carya* woodlands may dampen forest floor moisture, although impacts were only evidenced during winter sampling in this study. Diel sampling only occurred on two days and results are preliminary. Girdling of fire-sensitive midstory trees followed by burns resulted in drier litter during daytime sampling compare to an untreated control and a non-girdled site that was burned once. Sampling on both summer and winter days occurred following precipitation and litter moisture was quite high.

Effects of mesophication on litter flammability

In our laboratory flammability study, we found differential flammability between pyrophytic and mesophytic litterbeds and declines as mesophytic litter was added to reference pyrophytic litter. Increasing proportions of mesophytic species retained more moisture compared to pyrophyte-dominated litterbeds. SMC differed across all litter composition mixtures ($P < 0.001$) (Fig. 3, Drying Time = 0), increasing with greater proportions of mesophytes, averaging 256 %, 289 %, 348%, and 379 % for litterbeds comprised of 0, 33, 66, and 100 % mesophytic species, respectively. FMC at ignition differed across moisture treatments ($P < 0.001$) and litter compositions ($P < 0.001$), but with a significant interaction ($P = 0.006$). As at SMC, moisture content was greater in litterbeds comprised of increasing percentages of mesophytic species after both 12 and 24 h of drying, but not different when at EMC (Fig. 3). Litter depths differed across composition ($P = 0.036$), but post-hoc differences were not detected. Depth did not differ across moisture treatments ($P = 0.349$).

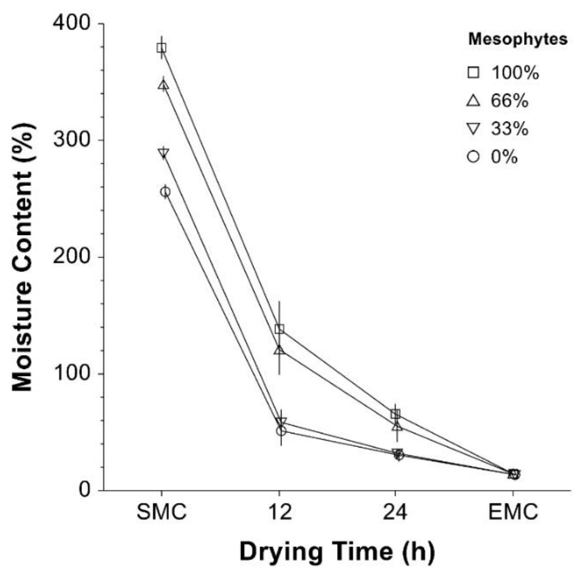

Figure 3. Moisture content of litterbeds varying in proportions of mesophytic versus pyrophytic species (%) at saturation moisture content (SMC), following 12 and 24 h of drying, and at equilibrium moisture content (EMC).

Combining correlated flammability metrics using PCA resulted in two factors explaining 81 % of the variability in the dataset, with Eigenvalues of 2.24 and 0.99 for Factors 1 and 2, respectively. Factor 1 explained 56 % of the dataset and was positively related to flame height, smoldering time, and litter consumption, with factor loadings of 0.91, 0.71, and 0.91, respectively. Factor 2 explained an additional 25 % of the dataset and was positively related to flame time, with a factor loading of 0.96. Litterbeds with increasing proportions of mesophytic species were less flammable than litterbeds composed of primarily pyrophytic species. PCA

Factor 1 scores (flame height, smolder time, consumption) differed across both moisture treatments and composition (P<0.001 for both), but with marginal evidence of an interaction (P = 0.053, Fig. 4). The two composition treatments with the least mesophytic litter (0 and 33 %) did not differ in flammability Factor 1, but litterbeds with 66 % mesophytic litter were lower than both 0 and 33 % mesophytic litterbeds. Litterbeds comprised of 100 % mesophytes were lowest in flame heights, smolder time, and consumption. When the moisture content of each litterbed was used as a covariate (P < 0.001), PCA Factor 1 differed across composition treatments (P < 0.001), but only litterbeds comprised of 100 % mesophytes were lower than the other three mixtures (Fig. 5).

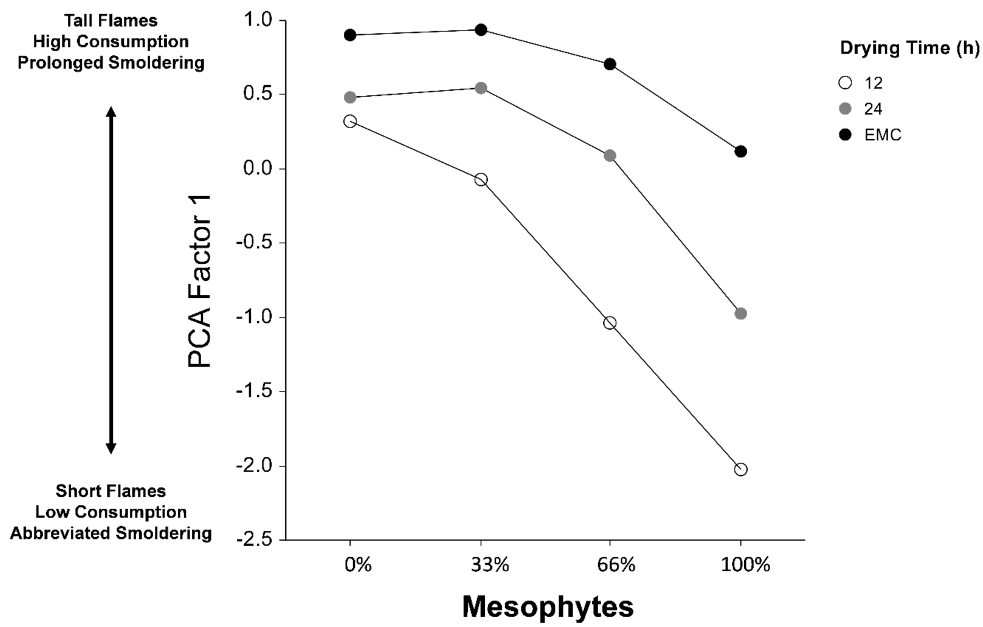

Figure 4. Flammability metrics (flame height, smolder time, consumption) combined through Principal Components Analysis across different litter compositions with varying amounts of mesophytic species (0, 33, 66, 100%) after 12 and 24 h of drying, following saturation, and at equilibrium moisture contents (EMC).

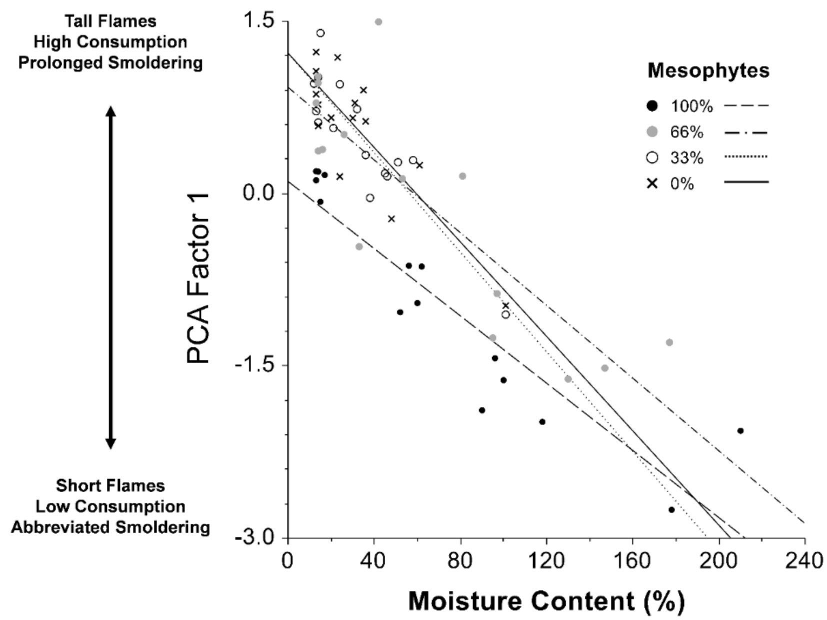

Figure 5. Flammability metrics (flame height, smolder time, consumption) combined through Principal Components Analysis of different litter compositions with varying amounts of mesophytic species (0, 33, 66, 100%) as a function of litterbed moisture contents at the time of laboratory burning.

The influence of litter from the mesophytes *Liquidambar styraciflua*, *Ulmus alata*, and *Cornus florida* in both fuelbed moisture retention and diminished flammability was demonstrated in these experiments. Changes in overstory composition resulting from encroachment by fire-sensitive mesophytes into pyrophytic *Quercus-Carya* woodlands may dampen fire behavior through incorporation of less flammable or fire impeding litter. In conjunction with direct and indirect influences of altered forest structure (e.g., increases in density and basal area, greater shade and decline of shade-intolerant herbaceous species, and inhibition of below-canopy winds), the impacts of shifting species composition on these once fire-prone ecosystems may result in loss of ecological function (Nowacki and Abrams 2008, Stambaugh et al. 2015) and difficulty restoring fire to these long-unburned ecosystems.

Response of overstory oaks to fire and thinning restoration treatments

The southern red oak tree-ring chronology included years of 1910 to 2015 (mean length of series = 68.4 years) while the post oak chronology spanned from 1853 to 2015 (mean length of series = 110.5 years).

Prior to implementation of recurrent thinning and burning treatments mean annual ring width for southern red oak for the time period 1992 to 2003 was similar ($p = 0.922$) between the thin+burn (2.2 ± 0.1 mm yr^{-1}) and control (2.3 ± 0.3 mm yr^{-1}) stands. Radial growth rates for post oak were also similar ($p = 0.309$) in the thin+ burn (1.2 ± 0.2 mm yr^{-1}) and control (1.5 ± 0.2 mm yr^{-1}) stands prior to treatments (1992 to 2003). Following initiation of restoration treatments, the mean annual ring width was approximately 25% greater for post oak in the control than in the thin+burn stand. For the first six years (2004 to 2009) after the initial treatments, the mean ring width for southern red oak remained nearly identical in the thin+burn and control stands. By 2010, radial growth for southern red oak in the thin+ burn increased such that the mean annual ring width for 2010 was 22% greater in the thin+burn than in the control stands. Radial growth rates for southern red oak continued to be greater ($p = 0.140$) in the thin+burn than in the control. Post oak radial growth was consistently greater ($p = 0.033$) in the control than in the thin+burn (Fig. 6).

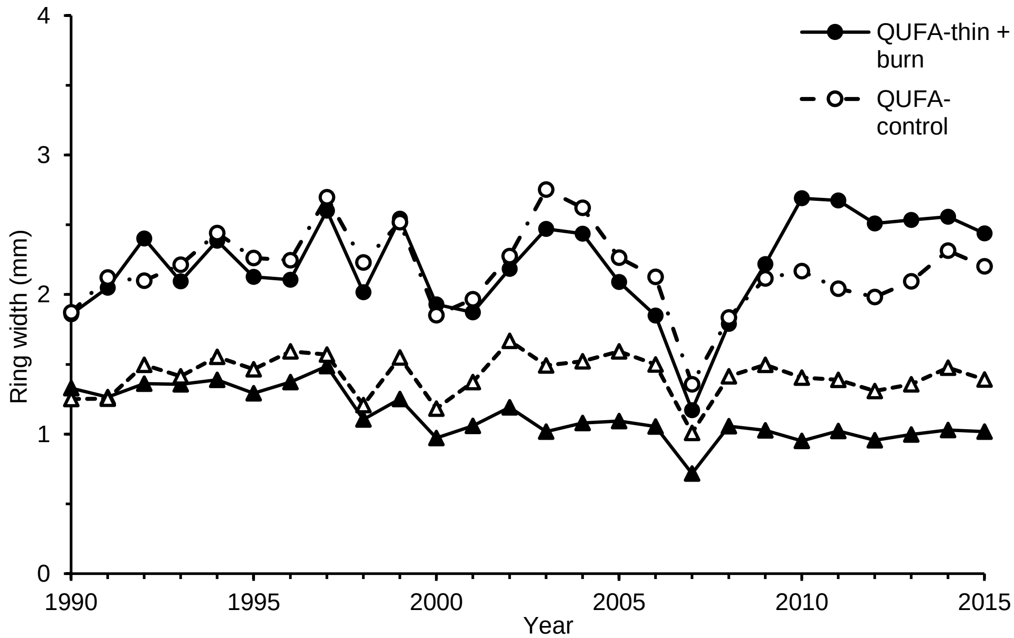

Figure 6. Ring widths of southern red oak and post oak 11 years prior to and 11 years after restoration treatments and controls at Strawberry Plains Audubon Center, Mississippi.

Southern red oak exhibited a slightly positive radial growth response in the thin+burn stand whereas post oak demonstrated a negative growth response. Southern red oak also demonstrated a greater growth response to the 2007 drought (Fig. 6). Post oak appeared to be more resistant to thinning, burning, and climatic disturbances in our study. Differences in growth responses are most likely attributed to species' life history strategies and characteristics. Longevity has been shown to be approximately twice as long (320 years) for post oak than southern red oak (150 years) (Guyette and others 2004). Other researchers have identified slower growth rates as tradeoffs to ensure longevity in post oak (Guyette and others 2004). Post oaks analyzed in this study were older than the southern red oaks. The increased age of post oak may have reduced the radial growth response identified. These results point to several lines of potential research that could help inform regional oak-hickory restoration.

Bark as a fire-adapted trait

Outer bark was thickest on the pyrophytes *Q. marilandica, Q. falcata*, and both *Pinus* species, and thinnest in the mesophytic species (*Prunus serotina* and *N. sylvatica*) as well as *Carya tomentosa,* which developed thick inner bark, but relatively thin outer bark (Fig. 7). The first axis of the PCA explained 48.4% of the variance and was positively correlated with wood area ($r = 0.46$), outer bark area (0.43), age (0.42), and total height (0.42) and slightly negatively correlated with height growth (-0.23) (Fig. 8). The height:bark relationships suggest that outer bark investment came at a cost to height growth, with fire-tolerant species devoting more to thicker and rougher bark and mesophytic species prioritizing height growth.

Our mixed model suggests that only the oaks and pines in our sample significantly reduced outer bark:wood ratio with increasing stem heights. All other species produced consistent outer bark regardless of height. Our results are consistent with previous studies on juvenile bark development (Graves et al. 2014; Odhiambo et al. 2014; Hammond et al. 2015; Shearman et al. 2018).

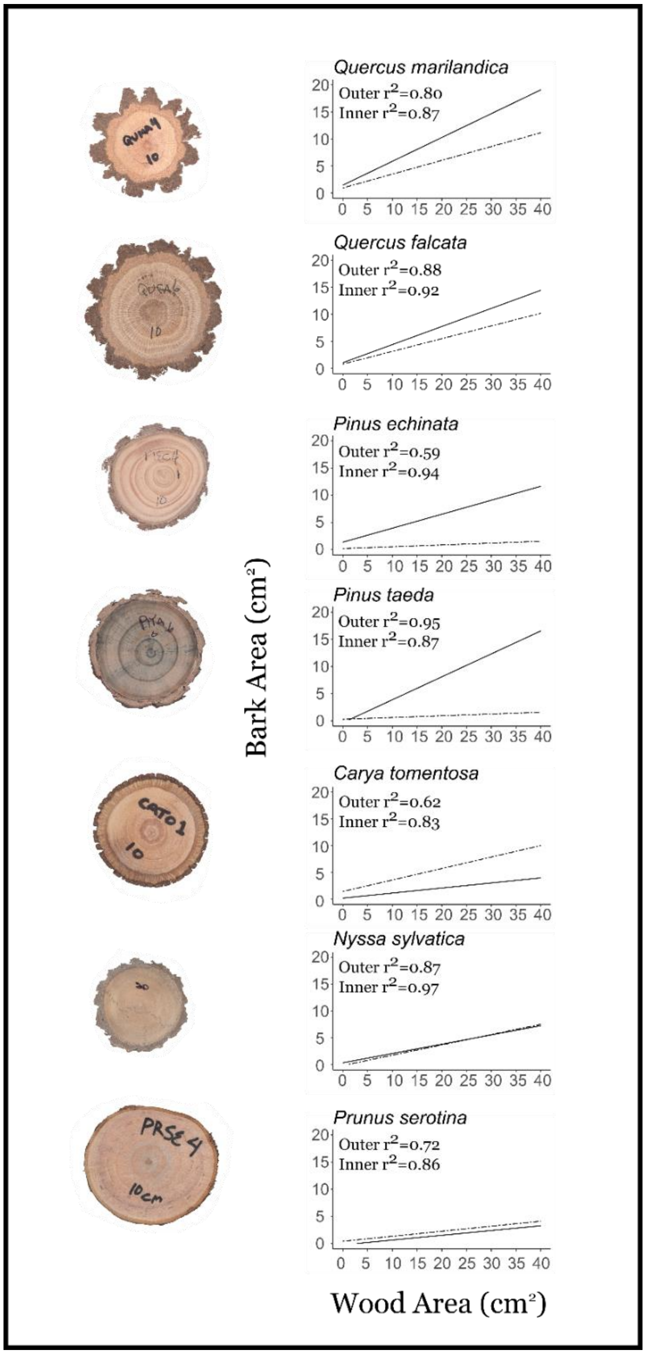

Figure 7. Relationship of outer bark (solid line) and inner bark (dashed line) area to wood area for seven different tree species. All regressions were significant at $\alpha = 0.05$.

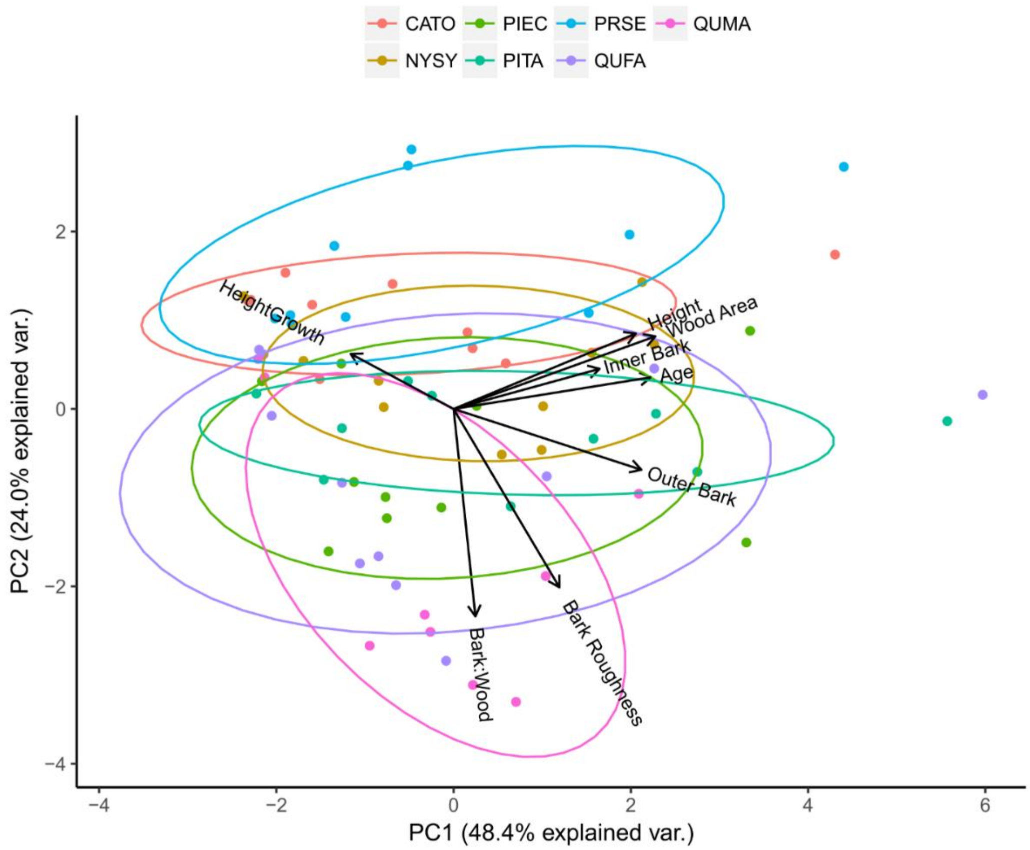

Figure 8. First 2 axes of a PCA on seven co-occurring tree species in the Tallahatchie Experimental Forest, Mississippi. Species are as follows: CATO = *Carya tomentosa*; NYSY = *Nyssa sylvatica*; PIEC = *Pinus echinata*; PITA = *Pinus taeda*; PRSE = *Prunus serotina*; QUFA = *Quercus falcata*; QUMA = *Quercus marilandica*.

Meta-analysis of fire-adapted traits

Oaks inhabit a diversity of sites across the southeastern US, exhibiting numerous fire-related protective, flammability, and physiological traits (Jacqmain *et al.* 1999, Cavender-Bares *et al.* 2004*a*). For pyrophytic oaks abundant in fire-prone pine-oak savannas and woodlands, there are clear advantages for traits that promote ecosystem flammability and protect stems from heating, despite the reduced growth potential (Kane *et al.* 2008, Veldman *et al.* 2013). The mesophytic oaks that lack fire protective and flammability traits tend to co-dominate in forests (in contrast to savannas or woodlands) where competition for light is acute and the probability of fires is reduced (Veldman *et al.* 2013). These mesophytic oaks have traits that confer rapid height growth, at the cost of developing traits that facilitate survival in frequently burned environments (Cavender-Bares *et al.* 2004*a*). Our analyses suggest that trade-offs (negative correlations) between flammability/protective traits and acquisitive physiological traits, as well as suites of positively correlated flammability and protective traits underlie observed suites of adapted traits and habitat preferences in oaks.

Pyrophytes in our analysis possessed protective traits such as rapid juvenile bark accumulation (Jackson *et al*. 1999, Graves *et al*. 2014, Hammond *et al.* 2015) and rapid wound closure

(Romero *et al*. 2009). Traits that promote flammability may enable pyrophytic oaks to increase local fire intensity while also injuring neighboring invaders that lack protective bark and wounding responses (Bond and Midgely 1995, Kane *et al*. 2008, Gagnon *et al*. 2010). The pyrophytes that invest in protective and flammability traits apparently do so through trade-offs in growth rates (Fig. 9, Hammond et al. 2015).

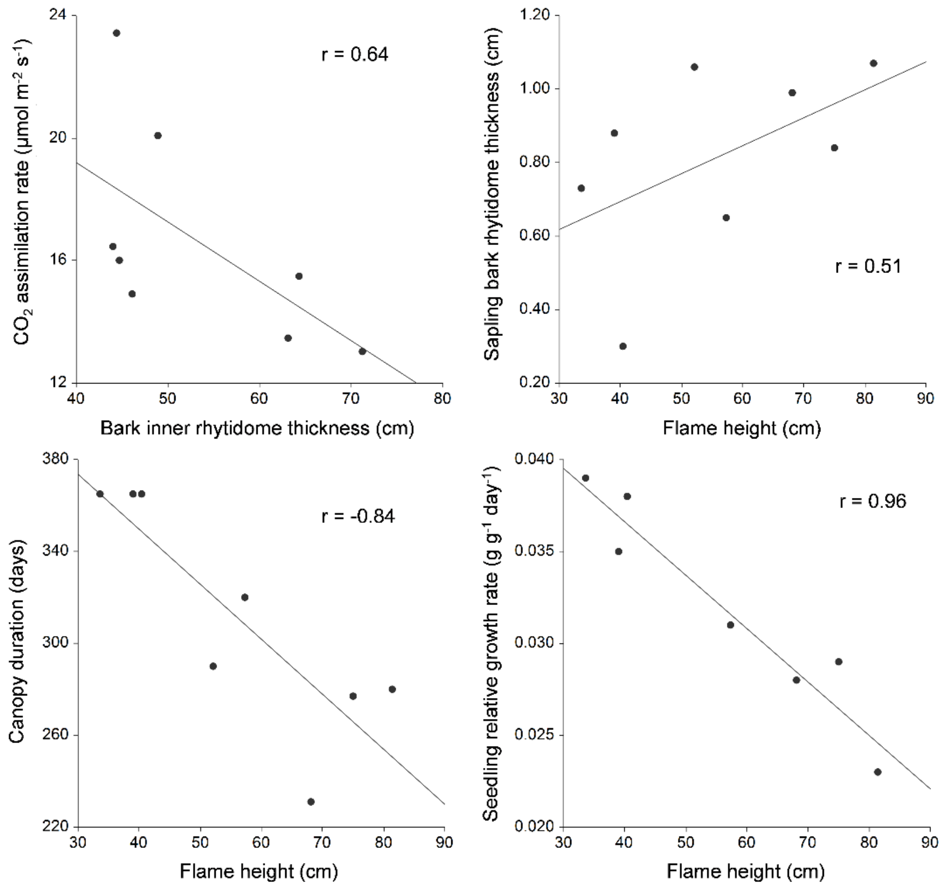

Figure 9. Correlations between flammability (litter flame height), protective (sapling inner bark rhytidome), and physiological (seedling relative growth rates and canopy duration) traits for eight southeastern oaks.

An alternative fire strategy is typified by the mesophytic oaks, enabling them to invade formerly fire-prone sites, and where established, to resist invasion by pyrophytes. These species impede rather than promote fire, and also lack protective adaptations that would allow persistence following fire. In frequently burned landscapes, these species dominate in fire-protected refugia (Platt and Schwartz 1990, Ware *et al.* 1993, Mola *et al.* 2014); where they are present in pyric uplands, these species are uncommon, short-lived, or persist as resprouts (e.g., Grady and Hoffmann 2012). Where fires are excluded, their dominance increases, often resulting in changes to community flammability and drastic shifts in community composition and structure, all of which are characterized by the positive feedback phenomenon termed “mesophication” (Nowacki and Abrams 2008). In addition to the lack of flammability and protective traits, these species grow rapidly and have long leaf lifespans (brevideciduous). In the southeastern USA, mesophication begins when fire-sensitive species establish during fire-free intervals and proliferate as fire is further excluded (Gilliam and Platt 1999). The consequences of fire exclusion for pyrogenic communities can be severe, with dramatic reductions in plant and animal biodiversity (e.g., Engstrom *et al*. 1984, Ware *et al*. 1993, Gilliam and Platt 1999, Hiers *et al.* 2007). These mesophytic oaks cause functional changes to pine-oaks savannas similar to the changes attributed to maples (*Acer rubrum* and *A. saccharum*) in fire-excluded eastern deciduous forests (Nowacki and Abrams 2008, Stambaugh *et al.* 2015). These mesophytic oaks (but not pyrophytes) should be primary targets for removal in ecological restoration of pine-oak woodlands in the region, yet many managers mistakenly target all oaks, due to a failure to recognize the functional roles of pyrophytes (Hiers *et al*. 2014). Our results emphasize the fire-related strategies of the pyrophytic southeastern oaks and should help clarify management that discriminates these species.

Most studies emphasize the importance of particular traits with clear associations with fire, however, we highlight that less intuitive traits are also essential and that multiple strategies contribute to persistence in fire-prone ecosystems. A better understanding of these traits and strategies are needed to manage and promote biodiversity in these and other fire-prone ecosystems.

Groundcover Vegetation Responses

Restoration treatments were effective at increasing groundcover plant species richness and plant density. Species richness and plant density were both significantly greater in treated plots than in adjacent control plots ($p = 0.013$ for species richness; $p = 0.038$ for log density), whereas they did not differ pre-treatment ($p = 0.437$ for richness and $p = 0.66$ for density). The treatments were generally effective at increasing the abundance of both open-habitat and forest species, while not increasing the abundance of ruderals. Weighted mean fidelity to open habitats was significantly greater in the treated plots than in the control plots ($p = 0.025$), in contrast to the lower fidelity pre-treatment. Examples of open-habitat indicators that responded positively to the restoration treatments included *Helianthus* spp. (including Ozark Sunflower [*Helianthus silphioides*], a regional endemic), panic grasses (e.g., *Dichanthelium boscii* and *D. laxiflorum*), and numerous native legumes, including *Desmodium laevigatum*, *Lespedeza repens*, *L. virginica*, and *Strophostyles umbellata*. Japanese honeysuckle (*Lonicera japonica*, a non-native vine somewhat indicative of forests and disturbed habitats), which dominated the groundcover, did not respond positively to the treatments. We found a positive effect of restoration treatments on little bluestem (*Schizachyrium scoparium*) and broomsedge (*Andropogon virginicus*), both of which are moderately indicative of disturbed habitats.

The non-native invasive grass, Japanese stiltgrass, increase in response to restoration treatments at both sites (Fig. 10). The way in which the increases occurred differed between sites ($p = 0.005$). At Wildflower, Japanese stiltgrass increased primarily as a result of increased density within two patches, whereas at Sharecropper the number of patches increased dramatically across the site.

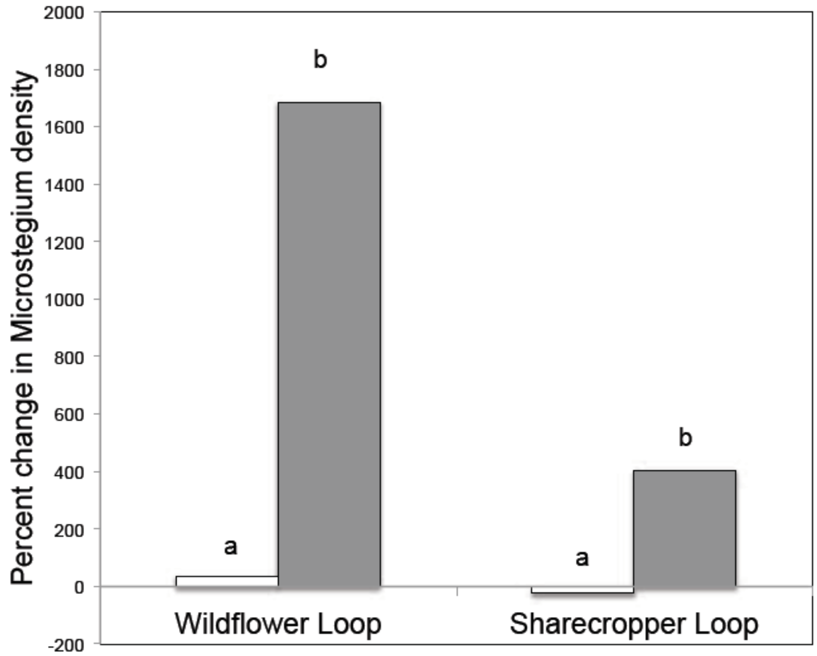

Figure 10. Change (%) in density of the non-native grass *Microstegium vimineum* in restoration treatments (filled) and in unburned controls (open).

In general, the results indicate that restoration treatments involving thinning of overstory and midstory trees combined with frequent burning increased the species richness and abundance of groundcover plant species indicative of fire-maintained open habitats. Canopy reduction and fire created the environmental conditions necessary to promote the natural increase of species indicative of fire-maintained open woodlands. Groundcover vegetation in the deciduous forests studied here was tolerant of low-intensity surface fires, perhaps because many species were perennials with rhizomes, deep taproots, or belowground bud/seed banks that were protected from damage by such fires (e.g., *Helianthus*, *Desmodium*, *Lespedeza*, *Dichanthelium* spp.). As a group, forest and open-habitat indicators were more likely to show positive flowering responses to canopy damage than were ruderals indicators (Brewer et al. 2012). Taken together, these results suggest that many groundcover plant species in oak-hickory-dominated forests of northern Mississippi are tolerant of canopy openings and low-intensity surface fires that are dominant components of regional restoration activities.

The positive response of the invasive non-native grass, Japanese stiltgrass, is consistent with the findings of previous studies and is definitely cause for concern. Proliferation of patches in response to restoration treatments was much greater at the site with a more recent history of agricultural disturbance (Sharecropper). The lack of replication of sites with different land use histories, however, precludes drawing any definitive predictions regarding how the response of Japanese stiltgrass to restoration treatments will vary among sites. Native vegetation located within patches of Japanese stiltgrass appeared to respond negatively to Japanese stiltgrass, as indicated by a reduction in native species richness in relation to the product of Japanese stiltgrass density and patch age. Given the beneficial effects of fire restoration on plant diversity in upland hardwood forests, the potentially negative effects of Japanese stiltgrass on plant diversity in upland forests may be greater than previously realized. Given limited resources, sites that are heavily infested with Japanese stiltgrass should be the lowest priority for restoration of fire-maintained open oak-hickory woodlands. Alternatively, for sites that have not been recently disturbed, that lack Japanese stiltgrass and that contain remnant populations of open woodland indictors, selective canopy thinning and repeated prescribed burning could be a practical and effective means of restoring plant diversity and desired species composition over the long term.

Fire and tornado effects on groundcover

In contrast to what was observed before the tornado in 2006, in 2009, after the tornado, but before the 2010 fires, groundcover plant species richness in severely-disturbed subplots was significantly greater than in subplots that were not severely disturbed ($P = 0.014$). The weighted summed abundance of open habitat indicators and ruderals was also greater in severely-damaged subplots than in undamaged subplots ($P = 0.049$ and $P = 0.012$, respectively). Examples of important open habitat indicators included Bosc's panicgrass (*Dichanthelium boscii*), creeping lespedeza (*Lespedeza repens*), hairy lespedeza (*L. hirta*), small woodland sunflower (*Helianthus microcephalus*, an oak woodland endemic), smooth ticktrefoil (*Desmodium laevigatum*), and Atlantic pigeonwings (*Clitoria mariana*).

Tornado and fire combined to increase the species richness and abundance of groundcover plant species indicative of fire-maintained open habitats and severe anthropogenic disturbance. The increase in species richness resulted in large part from increased occurrence of annual ruderals and short-lived perennials, which is not a desirable response in the context of maintaining the biotic distinctiveness of upland oak-pine ecosystems. On the other hand, tornado damage also increased the abundance of species indicative of rare, fire-maintained open habitats (e.g., Bosc's panicgrass, creeping lespedeza, hairy lespedeza, small woodland sunflower, smooth ticktrefoil, and Atlantic pigeonwings; Brewer *et al.* 2012). The increase resulted from the fact that many of these perennial species were already present but at low densities but were most likely suppressed by shade prior to canopy damage.

Restoring fire to oak dominated ecosystems in the eastern United States has the potential to increase groundcover plant diversity, both in terms of increased species richness and, more importantly, increased abundance of regional endemics indicative of rare habitats. This and related studies above suggest that prescribed burning alone most likely will not substantially increase plant diversity in the short term. Ideally, frequent prescribed burning should be coupled with overstory canopy reduction, while being particularly mindful of minimizing disturbance of the groundcover vegetation when felling and/or removing trees (Brewer *et al.* 2012). In areas where timber harvest is not practical, prescribed burning could be implemented in anticipation of or following natural wind-throw disturbances (e.g., tornadoes, derechos, hurricanes) to restore groundcover vegetation of fire-maintained open woodlands. Alternatively, more intense prescribed fires that cause some overstory canopy damage might produce similar results to combined effects of fire and wind-throw damage.

Conclusions and Implications for Management/ Policy and Future Research

JFSP 13-01-04 investigated a wide diversity of fire-vegetation feedbacks in oak-hickory woodlands formerly common in the southeastern US. This broad topic of fire-vegetation feedbacks has had increased recent attention globally and this research effort adds to several important aspects. Synthesizing these studies, it is clear that ecological restoration treatments involving prescribed fire shift fuels composition and structure toward a condition of functional restoration in these fire-prone communities. Overstory removal and return of fire decreased the contribution of mesophytic tree litter, retained pyrophytic litter, and increased the relative abundance of pyrophilic herbs (Brewer et al. 2015, Hammond and Varner 2016). These shifts resulted in lab and field fire behavior that was more intense, fast spreading, with potential effects that are capable of restoring the composition and structure of these ecosystems more broadly (Varner et al. 2015b, Kreye et al. *In press*). Our results on bark and fire-adapted traits reveal strong differences between historic species and contemporary invaders (Varner et al. 2016b). The two groundcover studies at both sites echoed these patterns, but focused on herbs (Brewer et al. 2015, Brewer 2016). These results provide multiple lines of evidence that fire and overstory manipulations can restore ecological function in oak-hickory woodlands (Stambaugh et al. 2015).

Two unforeseen results were found in our studies that have implications for restoration and for ecological research. First, the dramatic increases in a non-native grass (*Microstegium vimineum*) in response to burning and thinning was evident. The consequences of this grass invasion are dire for native plant diversity and ecological function (Brewer et al. 2015). Appreciation for the role of this plant and its success in prescribed fires is imperative in regional restoration efforts. Control measures following burning may become necessary in future restoration activities in the region. The other outcome was related to overstory tree release following restoration treatments. In contrast to common results of thinning and burning elsewhere, southern red oak and post oak did not experience dramatic growth surges following treatment and even declined in growth in areas (Kidd et al. *In review*). This contradictory finding is interesting and may be a product of a short period of analysis or may suggest that restoration treatments in these ecosystems may injure trees sufficiently to reduce vigor. Both of these findings are important and understudied aspects of restoration in oak-hickory woodlands.

Implications of the results to management and policy

Fire was and continues to be a major driver of plant community function and diversity in oak-hickory woodlands (Stambaugh et al. 2015). Contemporary prescribed fire in the region is challenged by external factors but remains a common land management tool (Ryan et al. 2013). Understanding how individual species and vegetation structure influence fire behavior and how the generated fire behavior influences the plant community is a major research and management pursuit. In these oak-hickory woodlands, fire and overstory thinning led to consistent changes in surface fuels, both herbaceous recovery and diminished mesophytic inputs. These changes to the surface fuelbed result in increased fire intensity that is capable of maintaining the current pyrophytic woody and herbaceous species while also killing or diminishing the presence of fire-dampening mesophytic woody and herbaceous species. Specific exceptions to this pattern were found for the presence and dominance of the non-native grass *Microstegium vimineum,* a serious threat to the continued use of fire in these ecosystems. Thoughtful management of this non-native grass will be necessary in future applications of prescribed fire across the sites where it is present, expanding, or potentially problematic.

Opportunities for direct implementation by end users

Prescribed fire remains an effective land management tool and this pattern was a theme of the several studies contained in this report. Prescribed fire without changes to overstory composition and structure failed to impact the groundcover and surface litter composition. The same result was found for sites with overstory manipulations without coincident burning. The combination of these two tools restored groundcover species richness, diminished mesophytic litter, reduced duff that can cause tree mortality and negative smoke and emissions, and facilitated the restoration of these oak-hickory woodlands. While considerably less research has focused on the use and effectiveness of fire in oak-hickory woodlands, these results echo a body of research that supports the role of fire in these ecosystems (Stambaugh et al. 2015).

An important caveat to the positive effects of fire in these ecosystems is the success of the non-native Japanese stiltgrass *Microstegium vimineum* in these ecosystems. This grass species increased dramatically following fire and overstory thinning and diminished local plant diversity where it was present. Management activities that 1) recognize this plant prior to burning and 2) seek to diminish this plant following fire and invasion will be critical to maintaining the overwhelming benefits of prescribed fire in oak-hickory woodlands and in other southeastern fire-prone ecosystems where Japanese stiltgrass invades.

Implications for future research

Several fuels and fire behavior research questions can be drawn from this research. There exists a need to understand how patchy herbaceous plants and litter fuels influence fire behavior. This work is not oak-hickory woodland-specific: the effects of variation in fuels on fire behavior is a major need for many fire-prone ecosystems (Hiers et al. 2009, Dell et al. 2017). This work should be prioritized where fires are used and the results incorporated into our understanding of fire behavior and effects. Our laboratory work suggests strong patterns in changes of flammability and need both validation in field settings as well as finer focus on how individual species influence ignition, intensity, and combustion residues. Incorporating the dynamics of fuel moisture, long recognized as a primary driver of fire behavior but less well-studied, will be of critical importance in both herbaceous and litter fuels (Varner et al. 2015a).

One implied objective of woodland restoration treatments is to improve the resilience of retained overstory trees. Our findings of muted or reduced vigor following restoration treatments should spawn future work on how common this finding is and how climate and fire injuries may stall restoration success. This work has implications beyond oak-hickory woodlands to other fire excluded ecosystems where overstory manipulations are prescribed.

The issues related to non-native plants and fire are complicated and often quite serious. Our findings of expansion and proliferation of *Microstegium vimineum* fit the worst-case scenario for prescribed fire effects. Past criticisms of prescribed fire in the region (e.g., Matlack 2013) focus on these shortcomings and negative consequences. Measures that may control or eliminate this species and other invasive species should be a major research priority for several fire-prone ecosystems where non-native species complicate otherwise beneficial ecological effects.

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Appendix A: Contact Information for Key project Personnel

J. Morgan Varner, Team Leader & Research Scientist
USDA Forest Service
Pacific Wildland Fire Sciences Lab
400 N 34th St, Suite 201
Seattle, WA 98103
julianvarner@fs.fed.us

J. Stephen Brewer, Professor
Department of Biology
University of Mississippi
412 Shoemaker Hall
University, MS 38677
jbrewer@olemiss.edu

Jesse Kreye, Research Scientist
School of Environmental & Forest Sciences
University of Washington
400 N 34th St, Suite 201
Seattle, WA 98103
jkkreye@uw.edu

Appendix B: List of Science Delivery Products

1. Articles in peer-reviewed journals

Varner, J.M., Kane, J.K., Kreye, J.K., Engber, E. 2015. The flammability of forest and woodland litter: a synthesis. Current Forestry Reports 1:91-99.

Brewer, J, Abbott, M.J., Moyer, S. 2015. Effects of oak-hickory woodland restoration treatments on native groundcover vegetation and the invasive grass, *Microstegium vimineum.* Ecological Restoration 33:256-265.

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Varner, J.M., Kane, J.M., Hiers, J.K., Kreye, J.K., Veldman, J.W. 2016. Suites of fire-adapted traits of oaks in the southeastern USA: multiple strategies for persistence. Fire Ecology 12: 48-64.

Kreye, J.K., Varner, J.M., Hamby, G.H., Kane, J.K. 2018. Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. Ecosphere In press. DOI: 10.1002/ecs2.2078 .

Shearman, T., J.M. Varner, and G.W. Hamby. Beyond bark thickness: measured bark roughness in seven co-occurring trees as a fire survival mechanism. In preparation.

Kreye, J.K., Varner, J.M., Hamby, G.H. Effects of restoration treatments on diel forest floor moisture in fire-excluded oak-hickory woodlands in Mississippi, USA. In preparation.

2. Technical Reports

3. Books, chapters

4. Graduate thesis (masters or doctoral)

Moyer, S.A. 2016. Competitive effects of increased plant species richness and increased endemic versus native generalist species dominance on the invasive grass *Microstegium vimineum* during oak woodland restoration. Thesis, University of Mississippi. 39 pp.

5. Conference or symposium proceedings scientifically recognized and referenced (other than abstracts)

Hammond, D.H., Varner, J.M. 2016. Fuel and litter characteristics in fire-excluded and restored northern Mississippi oak-hickory woodlands. In: Schweitzer, C.J., Clatterbuck, W.K. Oswalt, C.M. eds. Proceedings of the 18th biennial southern silvicultural research conference. USDA Forest Service, e-Gen. Tech. Rep. SRS-212. Asheville, NC.

Kidd, K.R., J.M. Varner, and J.S. Brewer. Radial growth responses of upland oaks following recurrent restoration treatments in northern Mississippi. Proceedings of the 19th Biennial

Southern Silvicultural Research Conference. USDA Forest Service General Technical Report eGTR-SRS-XXX. In review.

6. Conference or symposium abstracts

7. Poster

Toward a mechanism for eastern deciduous forest mesophication: the role of litter drying. Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J. Poster presentation at the 5th Fire in Eastern Oaks Conference. Tuscaloosa, AL May 27-29, 2015.

8. Workshop materials and outcome reports

9. Field demonstration/ tour summaries

Restoring fuels and biodiversity in fire-excluded oak-hickory woodlands. Field workshop at Strawberry Plains Audubon Center. Holly Springs, MS.

10. Website development

11. Presentations/ webinars/ other outreach/ science delivery materials

Fuel and litter characteristics in fire-excluded and restored northern Mississippi oak-hickory woodlands. Hammond, D.H., Varner, J.M. 2016. Oral presentation at the 18th biennial southern silvicultural research conference. Knoxville, TN Feb 18, 2014.

Suites of correlated fire-adapted traits in southeastern USA oaks. Varner, J.M., Kane, J.K., Hiers, J.K., Kreye, J.K., Veldman, J.W. Oral presentation at the 5th Fire in Eastern Oaks Conference. Tuscaloosa, AL May 27-29, 2015.

Impacts of species composition on litter flammability: a potential role in the mesophication of eastern U.S. hardwood forests. Hamby, G.W, Kreye, J.K., Varner, J.M. Oral presentation at 7th Association for Fire Ecology International Fire Congress. Orlando, FL, USA, Nov 28 – Dec 2, 2017.

Radial growth responses of upland oaks following recurrent restoration treatments in northern Mississippi. Kidd, K.R., J.M. Varner, and J.S. Brewer. Oral presentation at the 19th Biennial Southern Silvicultural Research Conference. Blacksburg, VA Feb 22, 2016

Appendix C: Metadata

All data described in the body of this report were submitted to the Forest Service Research Data Archive on 02 January 2018. With the departure of the PI from Mississippi State University, data storage transferred to the USDA Forest Service. The datasets in the archive include:

1. Influences of groundcover vegetation on forest floor fire behavior
2. Effects of fire and thinning on surface litter, woody, and duff fuels
3. Effects of fire and thinning on litter moisture dynamics
4. Effects of mesophication on litter flammability
5. Response of overstory oaks to fire and thinning restoration treatments
6. Suites of fire-adapted traits: Bark study
7. Effects of restoration treatments on native groundcover and *Microstegium vimineum*
8. Groundcover restoration with fire and a tornado disturbance